ON THE GENEALOGY OF PLANTS.

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ONE of the most remarkable anomalies, which the history of science and that of the human mind affords, is to be found in the appreciation which has been shown of the relationships which the different forms of life present. There has been no lack of acumen in discerning these relationships, in detecting the differences or recognizing the affinities, but there has been frequent failure to comprehend their meaning. The term relationship has been employed in a sort of metaphorical or metaphysical sense, as denoting mere resemblance wholly disconnected from any idea of natural dependence; as if the objects of nature were arbitrarily grouped into classes, orders and genera by the operation of some law of "pre-established harmony." It might be supposed that the term relationship, constantly in use in this sense, ought to have suggested the analogy to family, or *consanguineal* relationship among men, and led naturalists to seek to account for the resemblances observed among plants and animals on some such principle as that on which family resemblances are explained. Yet this simple deduction proved too profound for the human mind, and botanists and zoölogists went on accumulating facts down to the time of Lamarck, and most of them to that of Darwin, without perceiving their most obvious meaning. And there are still many who fail to perceive it, and who openly reject it when pointed out to them.

It is perhaps but proper to add that this state of things has not been wholly due to an inability to make rational deductions, but has been in part brought about by the existence of preconceived ideas which were sufficient to preclude all attempts to reason towards the true conclusion, however plain this course might appear to the unbiased mind.

But now that it is becoming generally recognized that the present forms of life are the true descendants of antecedent forms, and that the observed resemblances are the physical result of real or genetic relationship identical with that which makes children resemble their parents, it is but natural that old systems of classification should require to be entirely recast and moulded into harmony with this fundamental truth. Such, indeed, is the case, and already marked progress has been made, especially in zoölogy,

in which department chiefly, nearly all the most advanced workers in this field have concentrated their efforts.

In addition to other and greater benefits, this revolution has had the effect to relieve the systematists of the odium which naturally attaches to the apparently useless labor of classifying objects conceived as independent of one another. A dependence once established, classification becomes a vital process, and the only means of solving the highest of all scientific questions, that of the genesis of organic beings. Every fact in morphology or physiology, hitherto regarded too much as ends in themselves, now becomes an additional link in the chain of evidence which is to establish the genealogical history of a plant or an animal. Thus classification, formerly regarded as simply a means for the more convenient study of living things, becomes the highest object and chief end of biological investigation.

It is a matter of common remark that in the sudden advance of biological science which has taken place during the last eighteen years, it has been left for botany to bring up the rear. Prior to 1859 it was generally conceded that the science of plants occupied a considerably more advanced position than that of animals. This was due in the main to the impetus which it received at the hands of the Jussieus, who, following up the labors of Tournefort, had given to botany its so-called "Natural System."

But the Jussieus understood relationship only in the metaphorical sense, and maintained the fixity of species, and the system they established could not of course satisfy, in all respects, the law of genealogical descent. Its worst vice was the weighty authority which it acquired, and which became a serious barrier to its extension and rectification. But there are other reasons, existing in the nature of the two departments of biology, and which need not here be stated, that have contributed to permit our study of the vegetable kingdom to be outstripped by that of the animal kingdom. There has not, however, been wanting a deep sense of the inadequacy of the so-called Natural System of Plants, and in quite recent times its imperfections have become too obtrusive to be longer disregarded, even though greatly reduced by the labors of Lindley, DeCandolle, Hooker, Gray and others; and an effort has already been commenced, especially on the continent, to subject that system to a thorough criticism, with the aid of the new light which the modern school of biology has kindled in all its departments.

I do not propose in this paper either to review the literature of this subject, which is already becoming voluminous, or to attempt, among the many conflicting theories advanced, to reconstruct the natural system, but shall seek rather, in the light both of the new facts and the new principles already accepted, to state some of the objections to the received classification, and sketch, in its most general outlines, the form and direction which I conceive that the approaching reform is most likely to assume.

Probably the most objectionable feature of the system of classification proposed by Jussieu and still adhered to in nearly every systematic work on botany, is the position of the Gymnosperms. These constitute a sub-class of the Exogens and are made co-ordinate with the sub-class Angiosperms, which only embraces the Dicotyledons proper, or true flowering Exogens.

This arrangement and terminology involves a number of grave inconsistencies. In the first place the so-called Endogens or monocotyledonous plants are as truly Angiosperms as are the plants to which that term has been thus specially applied, the pistil consisting in both cases of a closed ovary. The Gymnosperms, therefore, in the present system are placed between the two great divisions of the Angiosperms and made to interrupt the natural series. The most casual observation, both of the foliage and the flowers, shows how awkward this position is, and indicates without closer scrutiny, that the Gymnosperms are out of place. Moreover, the enclosure of the germ is what chiefly distinguishes the phænogamic from the cryptogamic series, and the degree to which this is accomplished should mark the degree of advancement from the cryptogamic state. But we shall presently look deeper into this phase of the question.

In the second place, the reason assigned for the position of the Gymnosperms is the exogenous structure of their woody tissue. This argument might have some force if only the *Coniferæ* were embraced in the sub-class; but when we consider the *Cycadaceæ*, which equally belong there, a difficulty arises. Here the woody tissue assimilates almost altogether that of the endogenous palms or cryptogamic tree-ferns.

Again, the wood of the *Coniferæ* is by no means identical with that of the true Dicotyledons. It is destitute of the continuous vessels called ducts with their minutely porous joints, so characteristic of the former. The secondary wood consists, with the

exception of the medullary rays, entirely of large tubes, called *tracheïdes*, occupied with large prosenchymatous cells, which latter are nearly of uniform shape, while in the true Dicotyledons the tissue is in part parenchymous and the cells much more numerous and varied in form; moreover, the small circular areas enclosed between the walls of adjacent cells or *tracheïdes* are much more numerous and pronounced, especially in old tissue, in the *Coniferæ* than in the Exogens proper.

There is still a third important respect in which the Gymnosperms differ from the remaining Exogens in a marked manner. This is in the number of cotyledons, which is here usually more than two and sometimes as many as fifteen, while in true dicotyledonous plants the number is uniformly two; only a very few exceptions having ever yet been found; as, for example, in *Ranunculus ficaria*, which usually has but one, and in some species of *Phaseolus*, which sometimes have a whorl of three.

The objections above enumerated to the position of the *Gymnospermæ* in the prevailing system are quite independent of any recent facts pointing to their origin and derivation, and would be equally applicable under the old metaphorical conception of relationship. It is, therefore, all the more strange that it should have survived so long and should have required the argument from descent to finally break it down.

Evidence of this nature, however, is not now wanting, and it very plainly points to the direct *filiation* of the Gymnosperms upon the Cryptogams. This evidence concerns two important sets of characters, the woody tissue and the reproductive organs. As regards the former the close resemblance of the *Cycadaceæ* to the arborescent ferns is very obvious from a glance at a cross section of each. If this character, therefore, possessed the importance which is claimed for it, it would be found more difficult to pass from the *Cycadaceæ* to the *Coniferæ* than from the latter to the Dicotyledons. And we shall hereafter see that great liberty has been taken in thus grouping the *Cycadaceæ* and *Coniferæ* together.

If we consider the *Coniferæ* alone there is one class of facts recently brought to light which possesses an unusual interest. The investigations of Prof. Williamson[1] have shown that the trunks of *Lepidodendron*, exhumed from the coal beds of England,

[1] On the Organization of the fossil plants of the coal measures. Phil. Trans., 1872.

exhibit a species of exogenous growth. This differs not only from that of the existing pines and from that of the true Exogens, but also from that now known to take place in certain monocotyledonous plants and constitutes a sort of fourth type. It consists, so far as understood, in the formation of a layer of growing tissue with dividing cells (*meristem*) around each fibro-vascular bundle, the continuous division of whose cells necessitates a radial or centrifugal increase of the entire stem. A similar structure on a small scale occurs in certain now living cryptogamic forms, as in *Botrychium*, *Isoëtes*, etc. This form of exogenous growth may perhaps be regarded as marking a transition from the endogenous structure of most cryptogamic stems to the form of exogenous structure which prevails in the *Coniferæ*, but which has not been transmitted to the branch from which, on the hypothesis of descent, the *Cycadaceæ* have been developed.

The transition in the reproductive system is far more obvious and remarkable. What is known as "alternate generation," so long familiar to zoölogists, is now found to prevail throughout the greater part of the vegetable kingdom. It is most apparent in the higher Cryptogams, especially in the mosses, ferns, *Equisetaceæ* and *Lycopodiaceæ*. In all these the final stage is the production of a plant or "generation" capable of developing spores, which are of both sexes, and produce the sexual plant. Among the vascular Cryptogams there are two orders, one the *Rhizocarpeæ* in the fern group, the other the *Ligulatæ* in the club-moss group, in which the final spore-bearing stage is sexually differentiated. These produce two kinds of spores, called respectively, from their relative size, *macrospores* and *microspores*, the former of which develops a female, and the latter a male *prothallium*, or sexual plant. This *prothallium*, which in most vascular Cryptogams is an object of considerable size, and which corresponds to the entire leafy portion of the mosses, liverworts and other cellular forms, continues to diminish as the degree of organization increases; the spore-bearing generation, on the contrary, increasing in a corresponding ratio; the large fronds of a fern representing only the seta and capsule, or fruiting portion of a moss. In the *Rhizocarpeæ* and *Ligulatæ*, whose macrospores and microspores indicate a higher organization, this reduction of the sexual generation is carried so far that the *prothallium* scarcely protrudes from the spore, or is wholly confined within it. Hoffmeister[1] has

[1] Vergleichende Untersuchungen, 1851.

long ago pointed out the true significance of these facts, and shown that we have only to continue this same process a step beyond what it has already reached in *Salvinia* and *Isoëtes* to arrive at the condition presented by the existing Gymnosperms, the *Cycadeceæ* and *Coniferæ*. Here the macrospore exists under the name of embryo-sack, while the microspores are the pollen-grains. The so-called *macrosporangia* of these highest Cryptogams thus correspond to the ovules[1] of the Phanerogams, while the anther-cells of these latter are homologous with the *microsporangia* of the former. The *prothallium* is readily traced to the Gymnosperms, especially in the fertile flowers, where it re-appears under the name *endosperm*, and constitutes the albumen or reserve material of the future seed — one of the finest examples in biology of the fundamental identity of the reproductive and nutritive functions. In the staminate flowers the *prothallium* may be considered as represented by the *pollen-tube* (the elongated cell that descends from the pollen grains into the ovary and fertilized the germ), although a careful study of the microspores of *Isoëtes*, in which one cell remains sterile while the rest develop the *spermatozoa*, may leave some doubt as to whether the homology is here quite complete. The greatest differentiation has gone on in the microspores; the microspores and the plants and organs bearing them, still presenting, in many cases, a striking resemblance. In the *Cycadaceæ*, for example, the anther-cells are sessile and single or in groups upon the lower surface of the broad filaments like the "fruit dots" on the back of a fern. In the *Coniferæ* the stamens are less leaf-like, but the pollen-sacks are often solitary and scattered over the under surface of the flattened filaments.

An interesting similarity also exists between the male aments of certain *Taxaceæ*, as in the yew and the juniper, and the spikes of *Equisetum*, the horse-tail or scouring-rush. In these cases it is said that nearly all the morphological homologies are satisfied.

In general it may be said that in all these respects the *Cycadaceæ* resemble most the group of true ferns, the *Coniferæ* proper (pines, firs, etc.), most the club-moss group (Dichotomes), and the

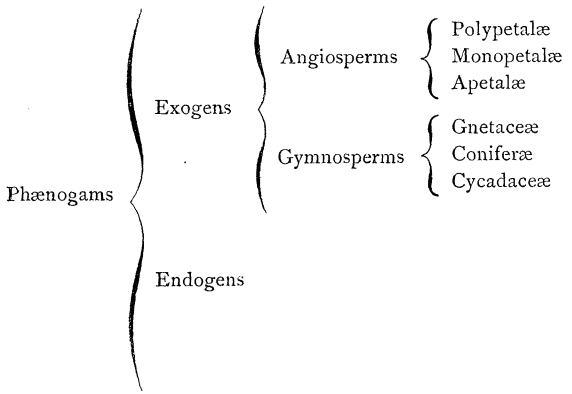
[1] Sachs (Yahrbuch der Botanick, 4 Aufl. S. 481) justly objects to the term ovule (or little egg) as entirely misleading in its etymology, and as tending to perpetuate the error that gave rise to its use, and proposes the term seed-bud (Samenknospe) as a substitute.

Taxaceæ, most the *Equisetaceæ;* a fact of great importance for the genealogy of plants, and to which we shall have occasion to refer again.

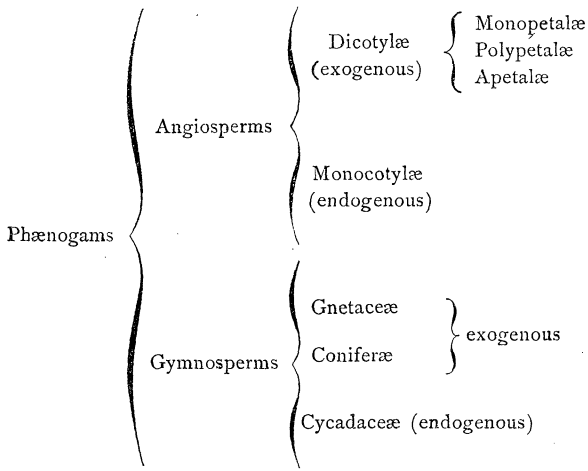
Upon the whole, therefore, it seems to be no longer open to serious doubt that both of these widely dissimilar orders of the *Gymnospermæ* (*Coniferæ* and *Cycadaceæ*), as also probably the *Gnetaceæ*, have been directly developed out of lower forms of cryptogamic vegetation. They should, therefore, certainly occupy a position at the base of the phænogamic series. Whatever may be ultimately accepted as the mode of transition from the Gymnosperms to the Angiosperms, it seems to be established that the former have actually descended from the latter, and they should therefore be all assigned a higher place in the scale of organization.

It is one of the misfortunes of botanical science that above the cellular plants no classification based on histological structure can be made; so nearly identical are the forms of structure through which all classes of vegetation pass. It is therefore necessary to depend in the main upon differences of the reproductive system, as affording the best characters by means of which to trace the development of vegetable forms. The Gymnosperms, no less than the Angiosperms, have both classes of structure, and we may almost say the same for the Cryptogams. But from the Cryptogam to the Gymnosperm, and from this to the Angiosperm, there is a continuous advance in one direction toward the complete protection of the germ as it is accomplished by the perfect ovary. It is indispensable, therefore, that all plants possessing this important character should be erected into one great group or class, and that from this group all plants to which this character does not belong be rigidly excluded. The terms *endogenous* and *exogenous* being common to both Angiosperms and Gymnosperms, should be excluded from the classification, or only employed to mark the subordinate divisions. The two systems of classification for the phænogamic series may therefore be thus compared:

OLD SYSTEM.



NEW SYSTEM.



The terms *Monoctylæ* and *Dicotylæ* are preferable to *Endogen* and *Exogen*, for the Angiosperms, since they lead to no confusion with the class *Gymnospermæ*. In this classification the terms conform to the strict rules for definition, each being wholly exclusive of all the rest. The reason for transposing the *Polypetalæ* and *Monopetalæ* will be given in another paper.

Before proceeding to consider more especially the manner in which the Angiosperms may have been derived from the Gymnosperms, it will be necessary to glance once more at the nature of the cryptogamic vegetation from which we suppose the latter to have descended. And for our purpose we may conveniently divide it into three groups: 1st, the group of true ferns; 2d, the

group of the club-mosses; and 3d, the horse tail group, or *Equisetaceæ*. The first of these groups seems to have come down to us from the Carboniferous epoch almost in an unchanged condition, trunks of tree-ferns quite similar to those still found growing in tropical countries having been exhumed from the coal measures. The second group must be made to embrace the ancient *Lepidodendron*, which flourished so abundantly in that luxuriant age, and whose resemblance to both our club-mosses, and to the proper Conifers has been so frequently remarked. In this group, therefore, there must have been great degeneracy, as of it the forests of that period seem to have been chiefly composed, while nothing now remains but the low herbaceous and moss-like plants that form our *Lycopodiaceæ*.[1] To the third group belonged the famous Calamites of the coal beds, and these too have dwindled into insignificant rushes.

Such is in fact the fundamental division of the cryptogamic series, and is based as well upon differences of internal constitution as of external aspect. If we associate these three classes of Cryptogams, respectively, with the three orders of the Gymnosperms, *Cycadaceæ*, *Coniferæ* and *Gnetaceæ*, we shall be able to discern many remarkable resemblances which, while they may really signify nothing, are sufficient at least to suggest an hypothesis. In the first group, or that of the true ferns, we have in the existing *Rhizocarpeæ*, to which our *Azolla* belongs, and of which the genera *Salvinia*, *Marsilia*, and *Pilularia* have been carefully studied, an undoubted transition towards the general condition presented by the *Cycadaceæ*. It is not unfavorable to this theory of transition that the existing forms indicating it are small and humble plants. The slight differentiation of the sexless spore into the macrospore and microspore could of itself have scarcely given the new form a special hold upon its environment, and we may almost wonder that this intermediary stage should not have succumbed altogether, as all the later ones probably have done. But the true phænogamic or flowering state once reached, permanence was acquired, and with it the power of attaining a higher development. It is remarkable that this differentiation affected the reproductive system only, and has left the woody tissue and also the foliage of the fern and the Cycad to a great extent unchanged.

[1] In the Sunda Islands there is a Lycopod that attains a diameter of six inches and a height of twenty-five feet.

That the *Coniferæ* proper (*Abietineæ*) have descended from the second or club-moss group, seems even better established than that the Cycads have sprung from the ferns.

The affinities of the extinct *Lepidodendron* with this group have always been recognized. Those who claim for *Lepidodendron* a Coniferous character only strengthen this view by showing how closely the two groups approached each other in those ancient times. The Araucarian pine of the southern hemisphere is even now covered with scales over its entire surface, and presents no small analogy with the *Lycopodiaceæ* and with what is known to have been the character of *Lepidodendron.* We must, therefore, regard *Araucaria* as our nearest living representative of the early transition form through which the Pine family was derived from the Carboniferous Lepidophytes. And it is especially interesting to remark that it is just this Araucarian group of true Conifers which we find associated with the arborescent cryptogamic vegetation, and whose scaly trunks lie side by side with the equally scaly trunks of *Lepidodendron* in the coal formation—a fact which shows at how early a period the differentiation began, and how little progress has been made within the same group during subsequent geologic ages.

With regard to the great advance which must have been made in passing from the crytogamic to the gymnospermous reproductive system, the evidence has already been briefly referred to. To the *Rhizocarpeæ* in the fern group correspond the *Ligulatæ* in the club-moss group, in which the asexual spore is completely differentiated into the sexual macrospore and microspore. In this order the only two genera thus far known, *Isoëtes* and *Selaginella,* have been faithfully studied by the foremost botanists of Europe, and the facts repeatedly verified. Hoffmeister's generalization, which is of the highest importance and has been generally accepted, has already been adduced, and its direct bearing on the immediate question need scarcely be reaffirmed.

The origin of the *Gnetaceæ* is far more obscure, and indeed so few positive facts have been brought forward to establish it that all speculation may be pronounced idle. That there is considerable general resemblance between the genus *Ephedra* and certain branching species of *Equisetum,* cannot be denied, but this similarity of habit is not accompanied by any corresponding similarity of structure either in the tissue or in the fruiting apparatus, while

the few genera which have been grouped under this order vary enormously in everything but their mode of inflorescence. Whether they have been developed independently from the Cryptogams or have been off-shoots from lower Gymnosperms must therefore remain one of the problems of botanical science; but it is a problem, as we shall presently see, which derives its great importance from the special *rôle* which the *Gnetaceæ* have been made to play, as a connecting link between the Gymnosperms and the Dicotyledons.

The highest marks of organization in the vegetable kingdom are the exogenous structure and the encasement of the germ. These may be regarded as the two great ends towards which vegetal life is perpetually striving. One of these ends is attained by the *Monocotylæ* or endogenous Angiosperms; both of them have been secured in the *Dicotylæ* or exogenous Angiosperms.

Although most of the intermediate stages, from the naked-seeded Cycad to the closed ovary of the Monocotyledon, have been obliterated, or have not been discovered, the evidence is nevertheless abundant that such a transition has taken place. If we consider what may be called their *physiognomy* alone, the descent of the true palm from the sago-palm, or both from a common ancestor in the *Cycadaceæ* would seem in a high degree probable. The great divergence in the matter of floral envelopes may be accounted for on the supposition that the differentiation, as is known to be frequently the case, was chiefly confined to the reproductive system and only slightly affected other characters. The absence of intermediate stages in our existing flora could then be explained by the now well understood law of the ephemeral nature of transition forms. In fact the Cycad is itself a transition form connecting the Cryptogams with the true flowering plants, or Angiosperms, and as such it is doubtless a comparatively ephemeral state. So far as general aspect or physiognomy is concerned, the ordinary observer, without trained scientific insight, naturally and instinctively classes the palm, the sago-palm, and the tree-fern in one and the same group, little imagining that botanists class them each in such a widely different group. Language itself builds on so obvious a resemblance. What we call the sago-palm, connecting it with the higher type, the Germans call the palm-fern (*Palmfarn*), connecting it with both the higher and the lower types of vegetation. Should further study

of these forms, in the light of the broadest principles of classification, lead the technical botanist to a recognition of their genetic relationship, and thus bridge over the two great chasms in the vegetable series, it would not be the first time that vulgar observation has been found to accord with true science after a long period of unmerited disdain.

The fact that the leaves of the *Cycadaceæ* grow from a terminal bud like the palms, while they unfold from the circinate apex like the ferns, shows that this resemblance to both palms and ferns is not altogether fanciful or purely superficial; in fact their genetic development from the latter, as already shown, is established by other evidence of the most vital character based on the morphology of the reproductive organs. It is therefore probable that the *Cycadaceæ* are not only more nearly related both to the *Palmaceæ* and the *Filices* than is generally supposed, but that they are less nearly related to the *Coniferæ* than is implied by their position in the received system of classification.

The wood of the *Cycadaceæ*, as already stated, consists of a mass of sheathed fibres in a large central pith composed chiefly of large prosenchymatous cells, and if not identical with that of the palms and arborescent ferns, certainly resembles this far more closely than it does that of the exogenous Gymnosperms. The similarity in the mode of flowering without which such a position could never have been thought of, may perhaps have been accidental, the two widely divergent lines of vegetation passing through some of the same transition stages in their progress towards the ideal type of vegetal perfection. The evidence already adduced of the derivation of the *Coniferæ* from a distinct stock of Cryptogams, to which the *Lepidodendron* belonged, would seem to corroborate this view, and this quite independently of the real origin of the *Dicotylæ*. Nor should botanists despair of still finding plain traces, in the transformations of the floral organs, of the descent of the *Monoctylæ* from the *Cycadaceæ*, and with this view the embryological study of the *Palmaceæ* cannot be too strongly urged.

The proper origin of the *Dicotylæ*, notwithstanding their possession of a closed ovary in common with the *Monoctylæ*, is a problem which presents the gravest difficulties to the genealogical systematist. Their derivation from the latter, though not wholly without legitimate evidence, is far from established, and may have to be altogether abandoned. The facts which support this hypothesis may be thus briefly summed up:

The endogenous structure of monoctyledonous stems is of two classes. In the palms, as in the *Cycadaceæ* and arborescent ferns, the foliage springs from one terminal bud which attains its full development before expansion, after which no further lateral enlargement of the stem takes place. This may be regarded as the normal form of endogenous growth. But another form is found in the trunks of the arborescent *Liliaceæ*, as in *Dracena*, *Yucca*, *Aloë*, etc., which may be regarded as representing an advance in the direction of an exogenous structure. The stems of these tree-like *Liliaceæ* actually undergo increase in size, or radial growth, after emerging from the bud. This takes place by the formation of a growing tissue (*meristem*) within the outer bark at certain distances below the terminal bud, which increases in thickness for some time before passing into permanent tissue, and effects an enlargement of the stem on all sides. A cross section of one of these trunks reveals a number of rings of this modified tissue, some of which are far internal, though at the time of their formation they must have formed the inner bark of the tree.

Although this is clearly an advance towards the true exogenous structure, it seems to be rather by way of analogy than of direct progress, the same end (power of strengthening the trunk to resist the force of gravity and of the elements and thus to render greater size and longevity possible) being attained, but by the adoption of a somewhat different means.

There is another group of plants, wholly different from those just described, which also afford considerable evidence of forming a transition stage from the endogenous to the exogenous structure. These are the aquatic plants. Sanio observes that in *Potamogeton* and other aquatic and submersed Endogens, "an axial bundle extends continuously through the stem, the bundles from the leaves only subsequently uniting with it," "a condition," says Sachs, "quite anomalous in monocotyledonous plants, but also found in dicotyledonous water plants, particularly in the *Nymphæaceæ*." Such a condition found among aquatic plants is certainly very interesting in view of the probable aquatic character of all primordial vegetation, but whether these facts possess any real significance in connection with the question of the origin of the Dicotyledons still remains doubtful.

In the venation of leaves of monocotyledonous plants, which is usually parallel, there are to be observed marked approaches

towards the reticulated structure which prevails with the *Dicotylæ*. Every one is familiar with many cases of this kind, as in *Dioscorea*, *Goodyera*, etc., while on the other hand, approaches to the parallel venation sometimes occur in the *Dicotylæ* (*Plantago*, etc.).

A far greater difficulty is presented by the cotyledons; for while there are a few cases in which exogenous plants develop but a single cotyledon, I am aware of no case in which an endogenous Angiosperm has been found to develop more than one. It is, however, presumable that a more complete investigation of this question may reveal transition forms here as elsewhere.

Such are the principal facts thus far made known which tend to encourage the hope of ever tracing the higher class of Angiosperms back to an origin within the lower class.

Far more satisfactory is the evidence that the Dicotyledons have been developed out of the *Gnetaceæ* and perhaps indirectly out of the *Coniferæ*. The *Gnetaceæ*, a small but interesting family of only three known genera (*Gnetum*, *Ephedra*, and *Welwitschia*) possess all the marks of forming a true intermediate link. The flowers of both sexes are provided with a sort of half-envelope, called the *perigonium*, which surrounds and protects the anther-bearing filament in the male, and the solitary ovule in the female flower, and may be regarded either as a rudimentary ovary or as a rudimentary perianth.

It is worth remarking here that the chasm between the Gymnosperms and Angiosperms is at all points greater with respect to the floral envelopes (including the ovarian) than with respect to the process and true organs of fertilization. The ovary of the Angiosperm is enclosed in an envelope, in the true Gymnosperm it exists but is exposed, in the *Gnetaceæ* it is half enclosed and half exposed. It matters not whether the *perigonium* be regarded as the homologue of the ovarian envelope or of the outer floral envelopes of the Angiosperms, since all the floral organs, including even the essential ones (stamens, pistils, etc.) are simply modified leaves. In the passage from the *Cycadaceæ* to the *Palmaceæ* no such connecting link has yet been discovered, and for the truth of such a transition we must rely upon the remarkably strong physiognomic resemblance coupled with the evidence furnished by the structure of the tissues and the mode of æstivation. The *Gnetaceæ*, however, while they give us this invincible evi-

dence of a transition in the rudimentary ovary, would seem at first view to afford no physiognomic mark to indicate the point at which the chasm was bridged over. There is one family of Dicotyledons, however, which, though little familiar to the inhabitants of the northern hemisphere, are none the less likely to have completed this transition, and in which there certainly is a strong physiognomic resemblance to at least one genus of the *Gnetaceæ*. Humboldt,[1] speaking of the remarkable form of the *Casuarineæ* of the East Indies, describes them as "trees with equisetum-like branches," and remarks that "Plumier's *Equisetum altissimum*, and Forskal's *Ephedra aphylla* of North Africa, are forms nearly allied to *Casuarina*." This physiognomic resemblance of *Ephedra* to both *Casuarina* and *Equisetum* is certainly very interesting, not only as affording a provisional hypothesis for explaining the transition from the Gymnosperms to the *Dicotylæ*, but also as marking out a line of investigation with a view to determining the origin of the *Gnetaceæ*. But to this we shall revert.

Not only do the *Gnetaceæ* thus approach the *Dicotylæ* in their reproductive system, but they also present a corresponding advance in the formation of the secondary wood from the structure of the *Coniferæ* towards that of the true Exogens. Besides the *tracheïdes* of the former it also contains vessels closely resembling the porous ducts of the latter.

Should the descent of the *Dicotylæ* from the *Gnetaceæ* be accepted as probable, it would only remain to determine the origin of the latter in order to complete a rough outline of the entire genealogy of vascular plants.

As already remarked, the attempt to affiliate them upon the *Equisetaceæ*, as a third independent branch of the Cryptogams, cannot be seriously made in the present state of science, notwithstanding the singular harmony in the general aspect of *Ephedra* and *Equisetum*. The fact heretofore pointed out, however, that a striking analogy subsists between the spikes of *Equisetum* and the male aments of *Taxus* and other allied genera, may be taken as a faint indication of what may have been the mode of development of these forms. It should at least be remarked that within the *Coniferæ* there is exhibited no small degree of progress towards certain leading characteristics possessed by the Dicotyledons. From the lowest to the highest,

[1] Ansichten der Natur, Stuttgart, 1871, p. 187.

from the Araucarian pines to the yew trees, such progress is well marked, and in *Salisburya*, the Japanese Ginkgo, which is related to the yew, the foliage comes at length to closely resemble that of many exogenous Angiosperms. The suspicion has even been expressed that all the genera of the *Coniferæ* may not have sprung from the same parent stock.

The origin of the *Dicotylæ*, which constitutes the chief problem in the genealogy of plants, is thus seen to be one which, while it admits of several possible solutions, nevertheless, in the present state of science, certainly admits of no positive solution. Whatever hypothesis we adopt, if we suppose a *monophyletic* origin for all plants, the derivation of both branches of the *Angiospermæ* from this common root will involve what may be thought to be a violent assumption. If the endogenous Angiosperms have developed out of the *Cycadaceæ* and the exogenous Angiosperms out of the *Gnetaceæ*, it requires some stretch of our credulity, in view of the bad repute into which all alleged "analogous" organs have in recent times fallen, to admit that the closed ovary, so identical in the two classes of plants, could have been arrived at from two such independent sources. To avoid this difficulty, which no one knows better how to appreciate, Prof. Hæckel suggests the probability that the Angiosperms as a class were first developed from the *Gnetaceæ*, and that subsequently they subdivided into the monocotyledonous and the dicotyledonous branches.[1] But with due deference to so high an authority, it is submitted that this would involve a still more violent assumption, viz: that an endogenous structure was derived from an exogenous one. Besides, we fail to find a single fact either in morphology or in palæontology to support this hypothesis. Again, if we seek to trace the genealogy of the *Dicotylæ* back through the *Monocotylæ* to the *Cycadaceæ*, we are driven to the equally forbidden presumption that the exogenous structure of the *Dicotylæ* and of the *Coniferæ* and *Gnetaceæ* was independently reached. There is, therefore, no serial line by following which all these difficulties can be escaped.

Those to whom all these instances of so-called "teleology" present no serious obstacle, may even find satisfaction in the conception that not only are the *Coniferæ* descended from two different parent stocks and the *Gnetaceæ* from still a third, but

[1] Schöpfungsgeschichte, Aufl. 5, Berlin, 1874, S. 430.

that the *Dicotylæ* may themselves be of heterogeneous origin, part of them being descendants of the *Coniferæ*, part, of the *Gnetaceæ*, and part, of the *Monocotylæ*. Should it ever become generally believed that the *Dicotylæ* are of multiple origin, the interest, now so great, in the true arrangement of the families of this class of plants would be greatly increased, and more satisfactory answers to many puzzling questions might be expected.

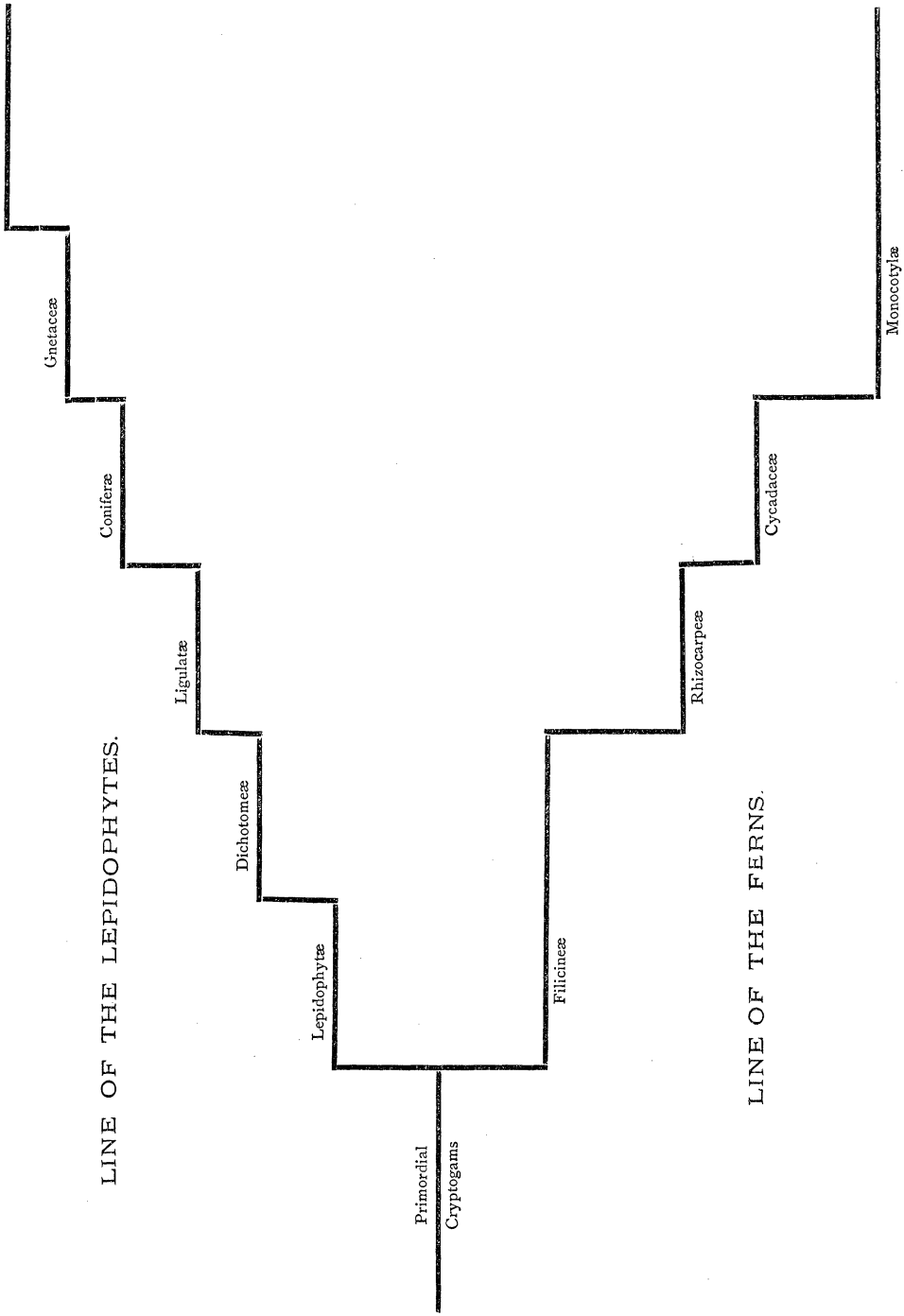
Perhaps the least objectionable of all the theories advanced, as that which requires the least extreme or improbable assumptions, and affords the greatest relief from the dilemma, is that which maintains the two great co-ordinate branches or parallel ascending series of the vegetable kingdom intact and independent from the most remote period to which they are traceable in the past history of the globe, and sees in the development of the endogenous and exogenous Angiosperms at the summit of each, respectively, the simple attainment in both of one of the great ends of vegetable existence, without which the highest functions of plant life cannot be manifested.

If we believe in the evolution of organic forms at all, we must accept that of vegetable forms, and if we are convinced that the higher plants are the descendants of lower ones, we ought by this time to have at least some provisional hypothesis as to the way in which this process of evolution has been going on in the vegetable world. We should not go on accumulating facts forever without attempting to make any use of them. In this age, when the law of descent has reached, in zoölogy, its exact stage, the stage of prevision and prediction, it is certainly time that some of the operations of this law were recognized and studied in the cognate kingdom of plants. The utmost that can be objected to any present attempt to trace the genealogy of plants, is, that the precise truth has not been reached, and those who are really competent to raise this objection must be competent to present a nearer approximation to the truth, which is the very service which science most needs. It is, therefore, with a full sense of the imperfection and inherent objectionableness of the scheme, and an entire willingness to see it superseded by one which shall better satisfy all the facts of science, that the one here rudely sketched is submitted. Stripped of all its complicating conditions and qualifications, many of which have been referred to and explained, this scheme of genealogy

may be more clearly presented by means of the following rough diagram, in which not only are all additional coördinate branches left unrepresented, but the continuation of each stage beyond the point of divergence is, for the sake of perspicuity, removed, leaving the differentiations only to stand in naked outline. This diagram presents the two great lines of descent, that of the Lepidophytes, of which we have the fossil genus *Lepidodendron* in the Carboniferous, and that of the ferns, trunks of whose arborescent forms are also found in the same formation. The line of the *Equisetaceæ* is omitted, although it probably had an independent existence, and may yet be found to have a genectic connection with some of the higher types.

The order of succession here laid down is confirmed by what is known respecting the time at which each of the several groups first appeared in the geological history of the globe. The primary divergence must have taken place in the latter part of the Devonian age, since within this formation occur some remains of *Lepidodendron*, while fossil trunks both of this and of true tree-ferns are found throughout the Carboniferous strata. It was in this latter epoch that both the ferns and the Dichotomes or Lycopodites attained their greatest perfection and abundance. Whether any of the large trees belonging to either of these groups had advanced to the stage now represented by the *Ligulatæ* and *Rhizocarpeæ*, there is no means of knowing, but that this stage was reached in both the great lines during the Carboniferous epoch must follow from our hypothesis, since it is within this epoch that both the *Coniferæ* and the *Cycadaceæ* first made their appearance, and during which they attained to very much the proportions and general character which certain forms of them still present. These forms advanced at a parallel rate and both reached the point of greatest development and supremacy at about the same time in the Triassic and Jurassic periods. They are both at the present time clearly on the decline, especially the *Cycadaceæ*, which are on the open road to early extinction before the march of higher types of vegetation. The palæontology of the *Gnetaceæ* is little known, but they have been supposed to have originated in the later Permian, or in the Trias. They constitute at best but a transition form, and are not sufficiently abundant to be likely to be discovered in a fossil state. It is a remarkable fact that the earliest remains of both the *Monocotylæ* and the *Dicotylæ* have been found

DIAGRAM SHOWING THE SUPPOSED LINES OF GENEALOGICAL DESCENT OF VASCULAR PLANTS.



in the same formation, viz: the Chalk, and although their first actual appearance may date back into the Jura or Trias, it is probable that in point of time the two great classes of Angiosperms had a nearly simultaneous origin. Whether either of these great vegetable types has reached its highest destiny on the earth it is impossible with certainty to affirm, but the indications are that, for the *Dicotylæ* at least, progress in organization is still going on.

In order to complete the systematic survey of the vegetable kingdom from the point of view of genealogical descent, the following logical scheme of classification is appended for comparison with the genealogical scheme presented on a preceding page: